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DIRECT BONE FORMATION IN THE ANTLER
TINES OF TWO OF THE AMERICAN CERVIDAE,
VIRGINIA DEER (*ODOCOILEUS VIRGINIANUS*)
AND WAPITI (*CERVUS CANADENSIS*)

WITH AN INTRODUCTION ON THE GROSS STRUCTURE
OF ANTLERS

BY CHARLES V. NOBACK, PHD., AND WALTER MODELL, B.S.

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BY CHARLES V. NOBACK, PH.D., AND WALTER MODELL, B.S.*

New York Zoological Park

Illustrations from photographs made in the Zoological Park

INTRODUCTION

(Figs. 1 to 56 incl.)

This paper is the report of a study of the gross and microscopic structure of growing antler tines in Virginia deer (*Odocoileus virginianus*) and the wapiti or American elk (*Cervus canadensis*). The major portion of the histological work was confined to a study of the tip of a growing wapiti antler. A similar histological study of the tip of a growing antler in the Virginia deer indicated that essentially the same process of growth is present in the growing antler tines of both of these American Cervidae. It is not our purpose to consider the general external structure such as the size and pattern of antlers, as this subject has been treated in works on natural history [Hornaday (18)].

A striking and impressive feature of antler-bearing Cervidae is that these large osseous structures are shed and renewed annually. One is impressed by the size and strength of these very rapidly growing osseous structures, which present perhaps the most rapid growth of membranous bone found in mammals.

Numerous descriptions are given of the number of tines or branches that antlers possess, and such terms as brow, bez, trez, royal, sur-royal and crown tines are frequently used in general descriptions of antlers. Aristotle (1) (384 to 322 B. C.) considered them as secondary sexual characters and noted that they were shed annually. "If stags are castrated before they are old enough to have horns [antlers], these never appear; but if castrated after they have horns [antlers], their size never varies, nor are they subject to their annual change." Redi in 1657 quoted by Owen (2) expresses the same

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opinion as Aristotle but gives no experimental data to support his views. In 1766 Buffon et Daubeton (3) in their "Histoire naturelle général" make the same statement regarding antlers and castration.

Prior to the nineteenth century, writers seem to have confined their records to descriptions of the general antler pattern, shedding, and the effects of castration. Since this paper will not deal with castration effects we will proceed to note some of the views that have been held on the structure and composition of antlers.

As late as 1758 Buffon (4) expressed the opinion that antlers were composed of wood, growing in a manner similar to the growth of the branches of a tree. Barr's (5) translation of Buffon's Works in 1807 contains the following reference on a red deer antler. "Its substance is perhaps more of the nature of wood than bone; it is, as it were, a vegetable grafted upon the animal." The velvet was designated as *écorcé* (bark). "Bois" is frequently used by the French to designate an antler.

The earliest references on the actual composition of antlers which we were able to find were those of Chevrueil (6) (1818) and Georges Cuvier (7) (1817). These writers were apparently the first to recognize and record the fact that the cervine antler is composed of bone. The former states that the antler of ruminants consists of bone and that on boiling, the organic matter is converted into gelatine, and that no fat is present. Cuvier (7) in an article under *Cerv* states, "antlers are composed of bone."

Johannes Müller (8) (1825) believed that the bony core of the ruminant horn and the antler are similar in structure, and considers the tubercle of the budding antler to consist of cartilage which ossifies in a manner similar to bones of the foetal skeleton. Gegenbaur (9) (1867) describes the ossification of the antler as an exceptional kind of cartilage metaplasia and agrees with Lieberkühn (10) (1864); who also believed that the antler was preformed in cartilage.

Landois (11) (1865) observed and recorded that the antler was not preformed in cartilage but in reality was a form of membranous bone. It remained for Robin et Herrmann (12) (1882) to confirm this finding and to present clear histological evidence as to the actual character and composition of the osseous structure of antlers. They gave a detailed description of the process of ossification and growth of the Roebuck (*Cervus capreolus*) antler from an undifferentiated connective tissue through a preosseous stage to membranous bone,

together with a description of the phases of osteoblastic development. They use the term preosseous substance (substance preosseous, or substance fondamentale de l'os de Müller) to describe the clear amorphous material containing osteogenic fibrillae which surrounds the osteoblasts.

Gadow (13) (1902) in a paper on "The Evolution of Horns and Antlers" emphatically denies direct bone formation in the antler and describes the presence (page 210) of "a dense layer of hyaline cartilage which together with the rapidly proliferating connective tissue. . . forms the growing point of the future pricket." He presents no original work in support of this statement. In reply to Dürst (14) (1902), who states that the bone of the antler is not formed by the intervention of cartilage, Gadow (13) states (page 222), "He [Dürst] and others will have to accustom themselves to the existence of cartilage in places where textbooks carefully abstain from mentioning it."

Fambach (15) (1909) in a critical review and by original work confirms the observations of Landois, Robin et Herrmann and Dürst on the structure of antlers.

Macewen (16) (1920) page xi, states, "The inquiry into the phenomena connected with the growth and shedding of the deciduous antler of the deer is undertaken to determine the data of a very interesting phase of nature which had not already been investigated, was imperfectly understood and which on its own merits, was of intrinsic value." Without referring to any previous work on the histogenesis of the bone in the antler he concludes from original work that (page 49). "The antlers showed a vigorous formation of bone through cartilage of the main stem and the basal portions of the tines, while the terminal parts of the same tines developed through direct bone formation."

Before going into a detailed account on the structure of antlers we feel it advisable to review the gross characteristics which differentiate the antler from the hollow horn of ruminants. The cervine antler is a deciduous bony protuberance arising from the pedicle of the frontal bone, covered with a true skin, the velvet, during its period of growth. This velvet is shed after ossification has been completed. Horns may be considered as the permanent keratogenous sheaths of ectodermal origin which enclose an osseous core arising from the frontal bone of the hollow-horned ruminants. Horns are present in both sexes, and except in the prong-horned antelope,

are never shed. The prong-horned antelope sheds its horns each year.

The males of all Cervidae with the exception of the Chinese water deer (*Hydropotes inermis*) are antler-bearing, while in the caribou (*Rangifer caribou*) and reindeer (*Rangifer tarandus*) both sexes bear deciduous antlers.

As the antlers of American deer are in process of growth from April to October, it will be realized that it is very difficult to obtain material for study without injury to the animal. The specimens used in this investigation were obtained from accidentally broken antlers.

GROSS EXTERNAL ANTLER STRUCTURE

At birth the antler-bearing young present no external indication of an ensuing antler. Several months after birth small paired bulges of the frontal bone, covered with the skin of the head, begin to appear anteriorly and laterally on the frontal bone. These bulges grow with marked rapidity to form the pedicle. The first antler grows from the tip of this pedicle when the deer is about eighteen months old. Ossification of the antler begins at the base and keeps pace with the growing tip, so that a section at any level is harder than that above it and less ossified than that below. Growth continues until the pattern of the species and individual is completed, ossification continuing until the tip has become ossified, after which the velvet is shed. The antler does not increase in diameter as it grows in length [Caton (17)] except at the corona around the base, which is the only region showing an increase in diameter. The external appearance of the annually recurring cycle of successive changes of the wapiti antler is illustrated in the accompanying series of photographs by Sanborn (20) (Figs. 1-16) and also described by Hornaday (18).

THE VELVET

The velvet which envelops the growing antler is an extension from the skin of the head (Fig. 23). After the antler has been shed it regenerates and grows from the adjacent cutaneous border to cover the tip of the pedicle. It is noteworthy that the velvet does not in any way resemble scar tissue but contains all the elements of cervine skin.

The velvet may be separated into three layers—an innermost

fibrous layer, the corium, and a peripheral epidermal layer (Figs. 17, 18 and 19). The fibrous layer, consisting of coarse collagen fibers arranged longitudinally, is quite vascular and gradually merges with the deeper undifferentiated connective tissue layer (Fig. 20). A few capillaries may be seen to pass from the fibrous layer of the velvet and to enter the layer of undifferentiated connective tissue in the region of the growing tip.

The corium (Figs. 17, 18 and 19) lies peripheral to the fibrous layer, containing hair follicles and sebaceous glands together with many fibrillae arranged in various directions, but most of the fibrillae are at right angles to the epidermal layer (Fig. 18). The hair follicles with the ducts of their sebaceous glands pierce the epidermis (Figs. 17 and 19). Paccinian corpuscles, Meissner's corpuscles, nerves and free nerve endings have not been demonstrated with hematoxylin and Orange G or Del Rio Hortega's silver carbonate method. The epidermal layer forms the outer coat of the velvet (Figs. 17, 18 and 19) and corresponds to the ectoderm (keratogenous layer) of skin.

GROSS INTERNAL ANTLER STRUCTURE

Figures 22 to 28 illustrate the gross internal structure of Virginia deer antlers in successive stages of seasonal growth. Fig. 29 illustrates the gross external appearance and Fig. 30 the gross internal appearance of the tip of the growing wapiti antler. (Old antler shed April 18, 1929; specimen obtained through accident July 2, 1929.)

The following description of the gross internal structure of the deer antler is primarily based upon a study [Noback (19)] of three antlers from the Virginia deer (*Odocoileus virginianus*) and the head of a Columbia black-tailed deer (*Virginianus columbianus*). These specimens were obtained at the New York Zoological Park during the summer of 1928. The first, an antler in early velvet, representing about two months' growth, was obtained on June 1, 1928. The second antler, representing a growth of about four months, came from a buck which died on July 25, 1928. The third, representing about six months' growth, was secured on October 4, 1928. The head of the Columbia black-tailed deer came from an old buck which died on January 28, 1929, four weeks after shedding its antlers.

In the latitude of New York, during late winter or early spring of each year, the mature antler is shed, after which a new one grows from the tip of the pedicle. The exposed surface of the osseous pedi-

cle (Figs. 22 and 23) is bare at the time of shedding. The marginal border of skin is the source of a cutaneous structure, the velvet, which soon envelops the free surface. While the velvet is developing, a mass of undifferentiated connective tissue, embryonic in character, is beginning to form. The growth of modified skin, the velvet, which later becomes covered with fine short hair, protects the connective tissue cap.

It may be noted that the pedicle is a cylindrical outgrowth from and a part of the frontal bone of the skull. The relation of the frontal bone to the pedicle is shown in Fig. 28. The blood supply of the pedicle is derived from the internal vascular system of the frontal bone.

A gross examination of the tine of a growing antler reveals that it is elastic in consistency while its cut surface presents a glistening bluish-white appearance which grossly resembles cartilage. Microscopic examination, however, reveals that the tip of the growing antler consists of a mass of newly formed undifferentiated connective tissue.

Growth of the antler seems to take place somewhat as follows: The cap of undifferentiated connective tissue "grows out" while the tissue at the base ossifies. Bone formation is more intense within the wall of the antler so that on examination we find that the wall of the cylindrical antler shaft is very compact in comparison with the interior. The interior of the antler is filled with a mass of soft bone tissue, a veritable network of fine blood channels which serve to supply the growing tip with an adequate amount of blood from the Haversian systems of the pedicle and frontal bone. The growing tip is primarily dependent for its nourishment upon blood received from the frontal bone through the pedicle and partly from the blood vessels of the velvet.

The gross internal structure of the tines of a young growing antler is illustrated in the accompanying photograph (Fig. 24) of a longitudinal section through a two months' growth of antler in velvet. The photographed specimen was secured on June 1, 1928 as the result of an accident. All the stages of growth in a growing antler tine may be seen in this photograph. A good view of the velvet and its hair may be seen in Fig. 25, a cross section from the beam of the antler where blood vessels in the velvet are plainly visible. The gross structure of the growing shaft is seen to consist of spongy bone richly

supplied with blood, while the wall consists of compact bone where calcification is more complete. The growing bone imperceptibly merges with the undifferentiated connective tissue.

A later stage illustrating the internal structure of a four months old antler is shown in Fig. 26. It will be seen that the clear tip has been practically replaced by new bone. It may be seen that the velvet covering the tip of the antler has begun to degenerate, as indicated by its darkening and drying out.

Figure 28 shows the internal structure of the mature antler, pedicle and frontal bone obtained by a longitudinal section. This antler is bare, free of velvet, and is composed solely of bone. The wall of the mature antler is seen to consist of hard compact bone while the interior still contains spongy, vascularized bone. The base of the antler is firm and compact, with a ring of bone overflowing the base to form the corona or burr. The line of demarcation between antler and pedicle is clear and distinct. It is along this line that separation from the pedicle takes place when the antler is shed and it is from this area on the pedicle that a new antler will grow. Complete ossification of a mature antler tip can be seen in Fig. 27.

Sections for microscopic study were obtained from the growing tip of a 75-day old wapiti antler. A close view of the exterior of the wapiti antler tine is illustrated in Fig. 29, showing the hair of the velvet very distinctly. The external appearance of an antler of essentially the same age can be seen on the wapiti in Fig. 12. A longitudinal section showing the gross internal structure of this antler tine can be seen in Fig. 30.

From within, the following three layers in the antler tine may be identified—a core of preosseous tissue in the process of ossification (Fig. 30), a layer of undifferentiated connective tissue, and the velvet. The layer of undifferentiated connective tissue is very thick at the tip where it forms a cap. It continues down the sides of the antler, gradually becoming narrower until it finally becomes imperceptible.

MICROSCOPIC STRUCTURE OF GROWING ANTLER TINE

The growing tines of a 75-day old wapiti antler and a two months' old antler from a Virginia deer were used to study the process of ossification in the tip of a growing antler. Del Rio Horteiga's silver carbonate method was used as a general staining procedure to

demonstrate cellular as well as fibrillar structure. A modification of this method was used to demonstrate the fibrillar network.

DEL RIO HORTEGA SILVER CARBONATE METHOD

1. Fix the tissue in a ten per cent. (10%) neutral formalin solution (excess of magnesium carbonate in formalin).
2. Cut sections, with a freezing microtome, 15 to 20 microns thick.
3. Wash the sections thoroughly in distilled water. A few drops of ammonium hydroxide should be added to the first wash water.
4. Sections are stained in the silver carbonate solution, which solution is prepared as follows:

Five (5) c. c. of a ten per cent. (10%) aqueous solution of silver nitrate (AgNO_3) [Merck] are added to twenty (20) c. c. of a five per cent. (5%) solution of sodium carbonate (Na_2CO_3) [Merck]. Without separating the precipitate add ammonia drop by drop until the precipitate is dissolved. Shake the beaker while adding the ammonia and be careful not to add too much. Finally add fifty (50) c.c. of distilled water and keep the solution in a dark brown bottle where it should keep well for several weeks.

The method of staining follows:

Wash the sections in a small Stender, then place them in ten (10) to fifteen (15) c. c. of the silver carbonate solution. Heat gently until a temperature of fifty (50) degrees Centigrade is attained or until the sections become yellowish brown. Discard the silver solution.

5. Before the silver solution cools, transfer the sections to distilled water and wash for from one-half ($\frac{1}{2}$) to one (1) minute.

6. Reduce the silver in a solution of fifteen (15) per cent. neutral formalin.

7. Wash thoroughly in distilled water. Examine under the microscope. If too pale place in silver carbonate solution again and repeat the whole procedure.

8. Tone with a two-tenths (0.2) per cent. aqueous gold chloride solution until grayish purple (five to ten minutes).

9. Wash in distilled water.

10. Fix with a five per cent. (5%) aqueous solution of sodium hyposulphite (sodium thiosulphite) for one to two minutes.

11. Wash very thoroughly in distilled water.

12. Run through alcohols 80%, 90% and absolute.

13. Clear in following solution:

Carbolic Acid crystals	5 grams
Creosote	50 c.c.
Xylol	45 c.c.

14. Mount in Dammar or Balsam.

The Modification which brings out the fibrillar structure consists of:

1. Fixation in neutral formalin (excess of magnesium carbonate in formalin) for at least a week.

2. Place in following solution for three days:

94 c.c. of a ten per cent. (10%) neutral formalin solution.

6 c.c. of concentrated Nitric acid.

3. Add two drops of concentrated ammonia to wash water.
4. The procedure given above is then followed.

Microscopic examination reveals an imperceptible merging of the fibrous layer of the velvet with the contiguous layer of undifferentiated connective tissue (Fig. 20). A definite line of demarcation between the undifferentiated connective tissue and the region of active ossification is present only where ossification is pronounced (Figs. 17, 31 and 32). A periosteum, as found in long bones, consisting of an outer fibrous restraining membrane with an inner osteogenic layer, is not present in the growing antler.

The undifferentiated connective tissue is composed of many layers of fusiform cells. These cells, with large dark, ovoid nuclei (Figs. 33 and 34), resemble those found in mysenchyma. For the most part, they are arranged parallel to the curvature of the cap. A delicate fibrillar network can be seen throughout this layer (Fig. 51), apparently continuous with the somewhat heavier fibers of the velvet. In lower sections along the sides of the ossifying core where ossification is distinct (Fig. 17), it is possible to measure the thickness of the undifferentiated connective tissue layer. In a cross section 3.0 cm. from the tip of the antler the undifferentiated connective tissue layer is 1.1 mm. thick; at 4.0 cm. it is 1.0 mm.; at 5.0 cm. it is 0.9 mm.; at 5.5 it is 0.75 mm. in thickness. These measurements indicate the gradual narrowing of this layer.

The presence of fusiform cells, with large, dark, ovoid nuclei, in the cap has been noted above (Figs. 33 and 34). Following a longitudinal section proximally, the aspect of these cells greatly changes (Fig. 43). They become larger, rounder and more granular, gradually losing their processes. Their nuclei which also become larger and rounder eventually assume an eccentric position in the cell. Longitudinal series of thin elongated cells with long darkly staining nuclei and lightly staining cytoplasm occasionally break through the layers of undifferentiated connective tissue cells just below the tip of the cap (Figs. 34 to 42). This series of cells seems to represent the evolution of the undifferentiated cell into an endothelial cell. The remaining cells are grouped around the evolving endothelial cells, so that in cross section 0.5 cm. to 1.5 cm. from the tip of the antler the appearance is presented of small masses of thin cells with lightly staining cytoplasm surrounded by the larger slightly basophilic cells. These actively proliferating basophilic cells derived from the undiffer-

entiated connective tissue of the cap possess fibroblastic characteristics.

In the lower sections these fibroblastic cells, enmeshed in a network of compacted fibrils, are more mature (Figs. 52, 53 and 54). Still lower (below 3.0 cm.) they show a clearing of cytoplasmic granules and signs of beginning atrophy (Figs. 43 and 55).

No spaces have been observed, in the masses of cells destined to form the endothelial lining of the blood channels, within two centimetres of the tip of the antler (Fig. 40). Below this level the developing endothelial cells gradually form the lining of the blood channels (Figs. 35, 36 and 42) which are continuous with the wider channels below, bringing blood from the vessels of the *dipl e* of the frontal bone.

Two centimetres below the tip, cells from the periphery proliferate toward the newly forming centres of ossification (Figs. 44 to 50). The type of cell from which they originate is apparently of the same morphological character as those found in the cap. Their evolution seems to be more rapid, i. e., the series of cells representing the phases of the osteoblastic development is shorter than the series in the development of the fibroblastic cells originating from the cap.

Differing slightly in shape, the cell derived from the periphery has the definitive form of the osteoblasts (Figs. 46, 50 and 56). It is smaller, more basophilic, and more polygonal than the cell from the cap. The fibroblastic cells from the cap seem to lay down the fibrillar framework which later becomes ossified, while osteoblasts from the periphery apparently pass to the newly formed centres of ossification. Mitotic figures are present in the cells of the undifferentiated connective tissue and rare in the region of the matured osteoblasts.

As mentioned above, the tip of the cap shows a delicate fibrillar network (Fig. 51). As the developing fibroblasts increase in size they separate, while the fibrillar network spreads out to enclose them within its meshes, the fibrils coalesce to form a coarser network (Figs. 52, 53 and 54). Centres destined to become blood channels are devoid of the fibrillar network but contain a few delicate longitudinal fibrils (Figs. 51 and 52).

As the fibrillar network becomes coarser, the enmeshed cells at first show slight and later marked atrophy, together with a gradual disappearance of cytoplasmic granules (Figs. 43 and 55). Slight but definite centres of ossification first appear two centimetres below the

tip of the antler, immediately deep to the peripheral undifferentiated connective tissue. In this region of ossification the fibrils, becoming heavier, coalesce, the enclosed cells apparently atrophying from pressure. An occasional enclosed osteoblast does not atrophy and becomes an osteocyte of the mature antler bone. The trabecular framework is apparently formed by coalescence of fibrils (Fig. 54), beginning just under the peripheral undifferentiated connective tissue gradually extending distally and centrally.

Osteoblasts seem to migrate from the periphery to the spaces between the endothelium of the blood channels and the surrounding preosseous ring (Figs. 50 and 56). The migration of the osteoblasts from the periphery to the centre is made possible by a continuity of these spaces. The osteoblastic migration through these spaces seems to be the mechanism by which central ossification takes place. The process of ossification continues peripherally so that the wall of the antler finally consists of compact bone while the central portion remains spongy.

The vascular system of the growing antler consists of simple blood channels which are not surrounded by concentric lamellae which characterize the Haversian systems of skeletal bone. This sharply differentiates the bone of the antler from that of the pedicle.

The content of the blood channels in the antler apparently consists solely of blood. We have not been able to demonstrate the presence of fat or hematopoietic elements found in the marrow of the diplœ of the membranous bones of the cranial vault.

Fibroblasts from the undifferentiated connective tissue cap lay down the ossifiable fibrillar framework while the osteoblasts from the periphery seem to complete the process of ossification.

The presence of fibrils in the matrix surrounding the fibroblasts and absence of cartilage during the entire process of growth leads us to conclude that the antler is a form of membranous bone.

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Fig. 1. *Upper.* The matured antlers of the wapiti are usually shed in March, occasionally in February. The exposed surface of the pedicle is shown after one antler had been dropped. Fig. 2. *Lower.* The appearance of the exposed pedicle tips after both antlers had been shed. Figs. 2, 9, 15 and 16 are used here for demonstration. The other figures are from the same animal.

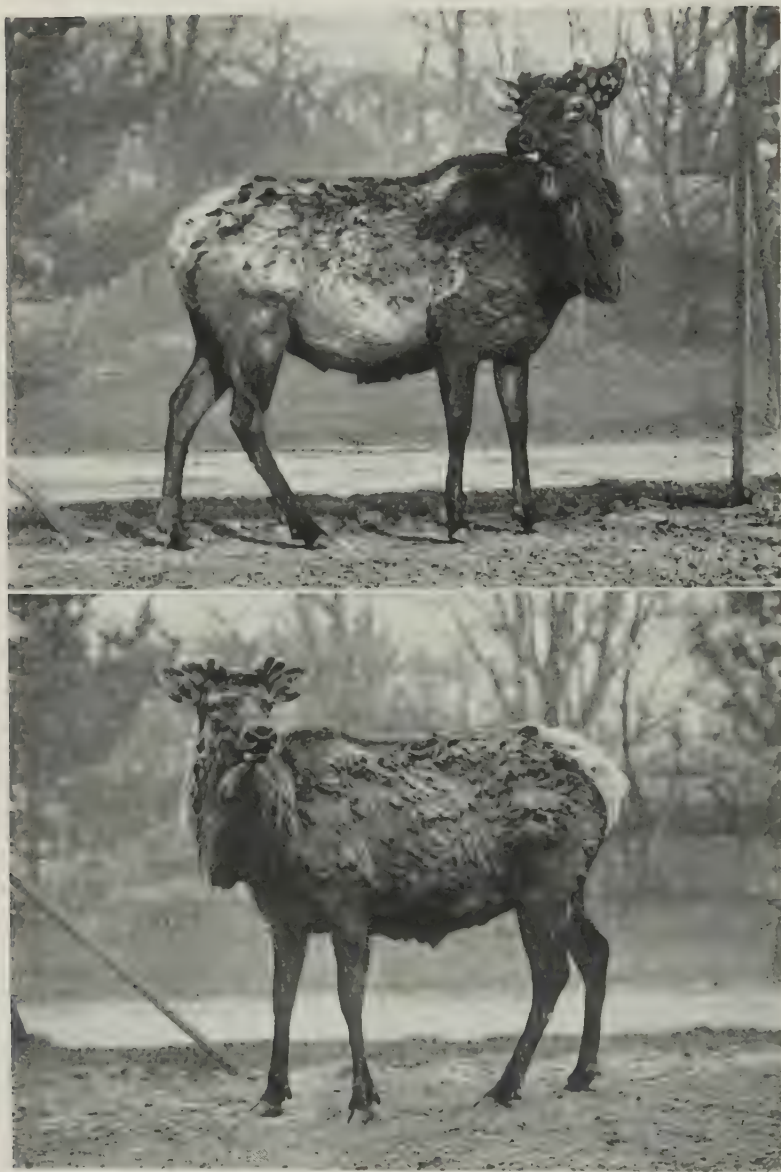


Fig. 3. *Upper.* Antlers budding from the pedicle, April 26.

Fig. 4. *Lower* The new antlers are beginning to show the branch-like form.



Fig. 5. *Upper.* The rapidity of growth is shown by the appearance of the antlers about the 5th of May. Fig. 6. *Lower.* The branching of the antlers indicates their future pattern; May 9.



Fig. 7. *Upper.* The growing antler structure shows increased division on May 16, and the rough coat of old hair is shedding out. Fig. 8. *Lower.* As the antlers approach their normal size, they become a prominent and striking feature of the male wapiti.



Fig. 9. *Upper.* During the period of development, while the antlers are in the velvet stage, the wapiti exercises the greatest care in avoiding hard objects. Fig. 10. *Lower.* The velvet masks the trim osseous structure of the antler.



Fig. 11. *Upper.* On July 6, the antlers are approaching the final stages of development. There is a noticeable shrinking of the velvet especially at the tips. Fig. 12. *Lower.* In midsummer, July 12, the antlers have attained their greatest length.



Fig. 13. *Upper.* The antler pattern is usually completed in August, and at this time growth has ceased and the final stages of hardening are taking place.

Fig. 14. *Lower.* When the antler has become completely hardened the velvet dries out and peels from the bony structure in long, thin ribbon-like strands.

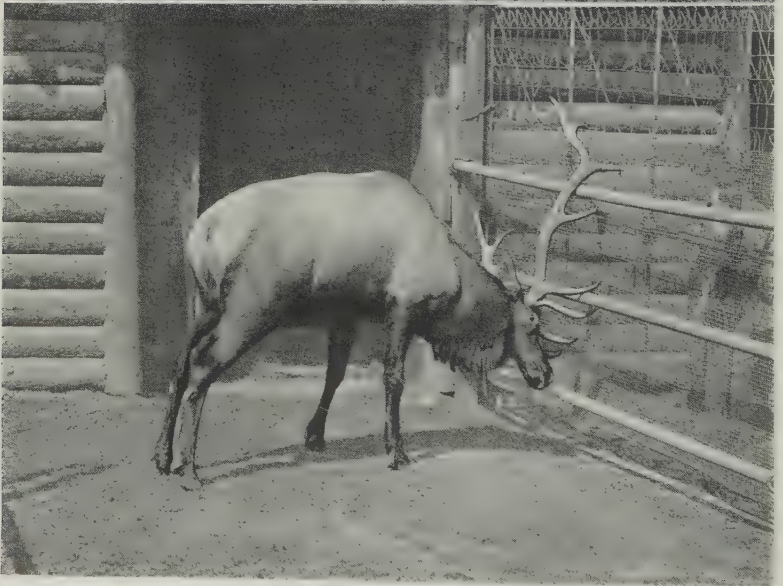


Fig. 15. *Upper.* During the early stages of antler development the animal is most docile. Fig. 16. *Lower.* When the velvet is shed and his old vigor returns, he then becomes very pugnacious and charges violently against any barrier.

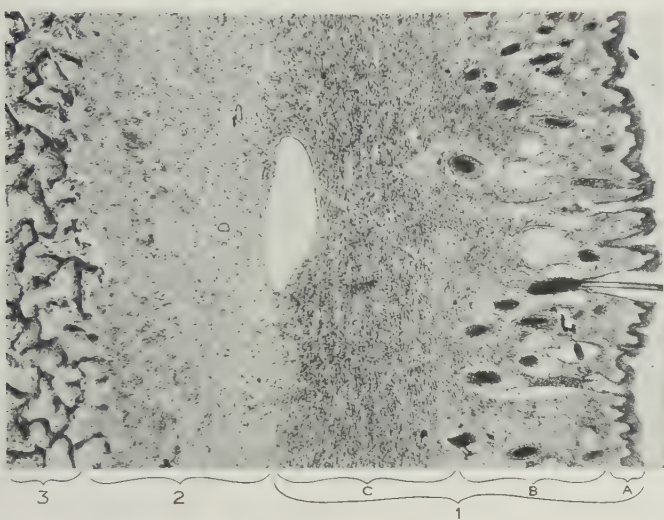


Fig. 17. Cross section of Wapiti antler, 5.0 cm. below tip. 1. Velvet; a. Epidermal layer; b. Corium with sebaceous glands; c. Coarse fibrous layer. 2. Undifferentiated connective tissue layer. The open space in center is a capillary. 3. Ossifying core. Obj. 48 mm. Ocular 8 \times comp.

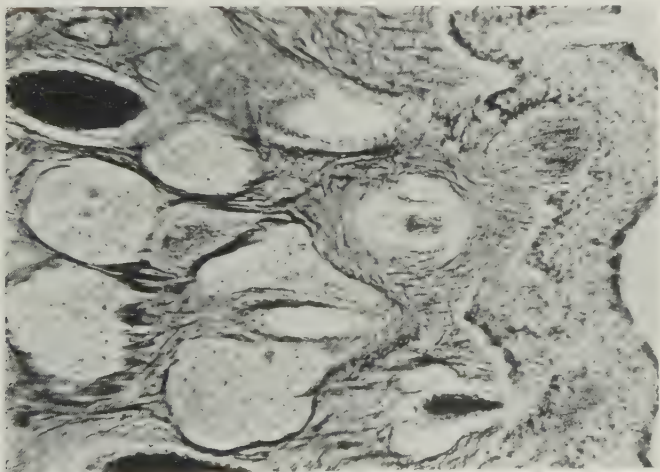


Fig. 18. Cross section of velvet showing fibrous structure of its corium. Obj. 32 mm. Ocular 8 \times comp.

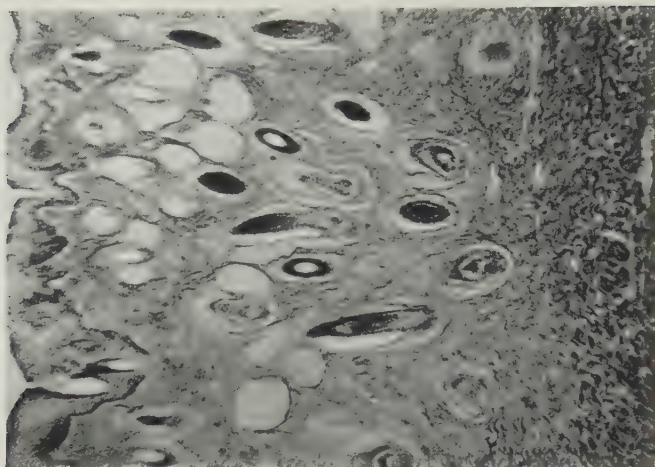


Fig. 19. Cross section of velvet. Obj. 32 mm. Ocular 8 \times comp.

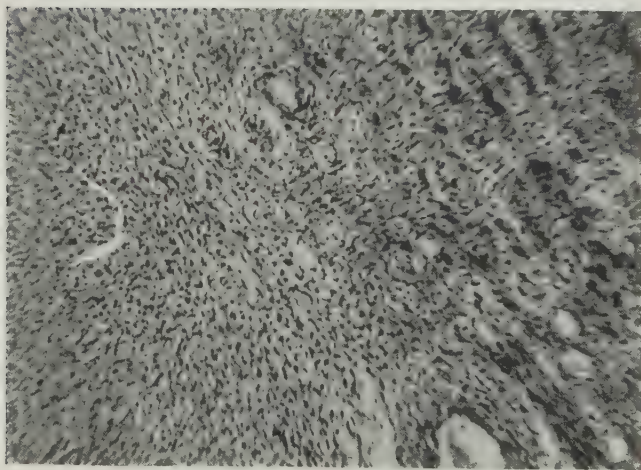


Fig. 20. Cross section of antler showing the merging of the undifferentiated connective tissue with the fibrous layer of the velvet on the right. Obj. 16 mm. Ocular 8 \times comp.

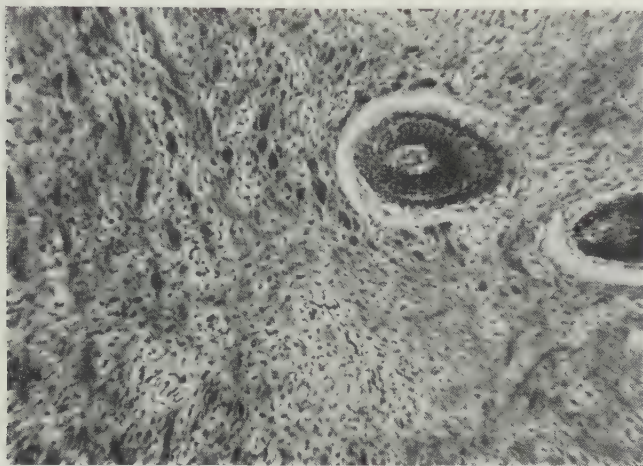


Fig. 21. Cross section of antler showing fibrous layer and corium of the velvet.
Obj. 16 mm. Ocular 8 \times comp.

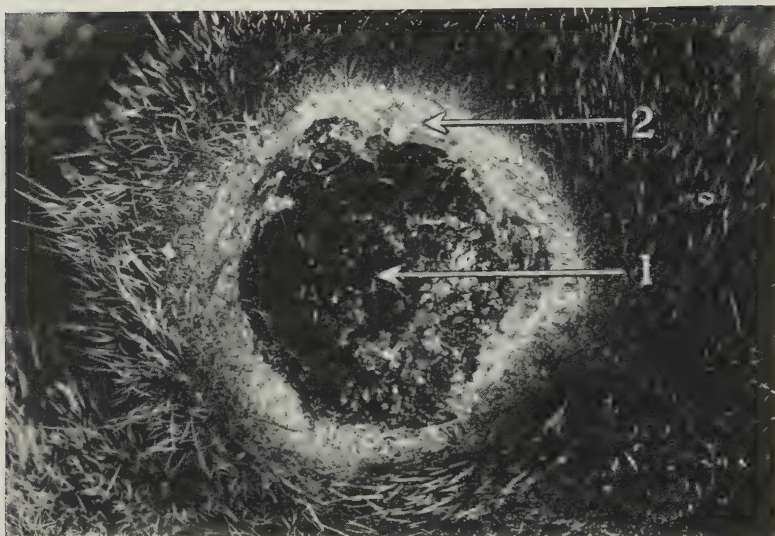


Fig. 22. Tip of pedicle of a Virginia deer two weeks after the antler had been shed. 1. A thin layer of dried blood, scab, covering the antler tip. Undifferentiated connective tissue, embryonic in character, is forming beneath the scab. 2. Edge of the pedicle skin surrounding the pedicle tip. The velvet, a form of skin, will evolve from this border to protect the delicate tip of the new antler.

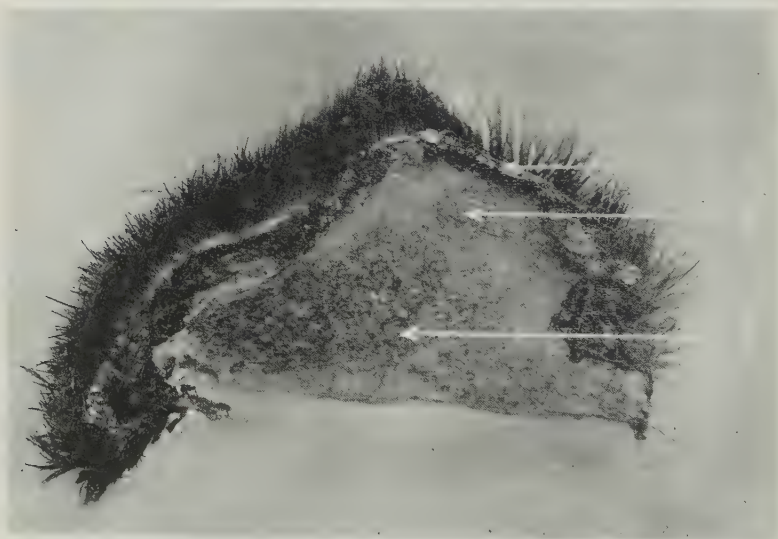


Fig. 23. A longitudinal section through the pedicle of fig. 22 (Virginia deer). 1. Frontal bone, from which the new antler will derive most of its blood supply. 2. The pedicle, a cylindrical growth of bone from and a part of the frontal bone; 3. A layer of dried blood covering the tip of the pedicle two weeks after antler had been shed.

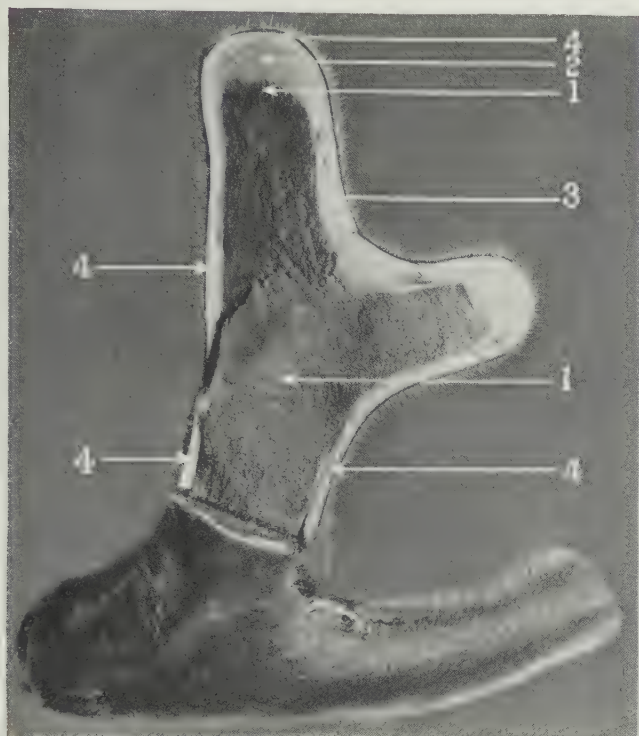


Fig. 24. Longitudinal section of a two months' old Virginia deer antler showing its gross internal structure. 1. The ossifying core of undifferentiated connective tissue, richly supplied with blood and containing areas in process of direct ossification together with spicules of newly formed bone; 2. Rapidly proliferating undifferentiated connective tissue, embryonic character, forming the growing tip of the antler; 3. Proliferating undifferentiated connective tissue continuing down the side of the antler tip; 4. The comparatively thick white border enveloping the antler is the velvet. The thin dark border of the velvet is the pigmented layer just beneath the hair.

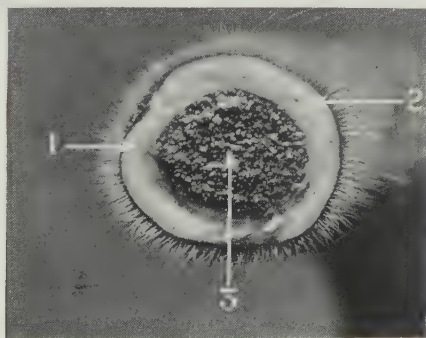


Fig. 25. Cross section of the two months' old antler of Fig. 24; 1. The velvet, a thick cutaneous structure; 2. A blood vessel within the velvet; 3. The ossifying core of undifferentiated connective tissue.

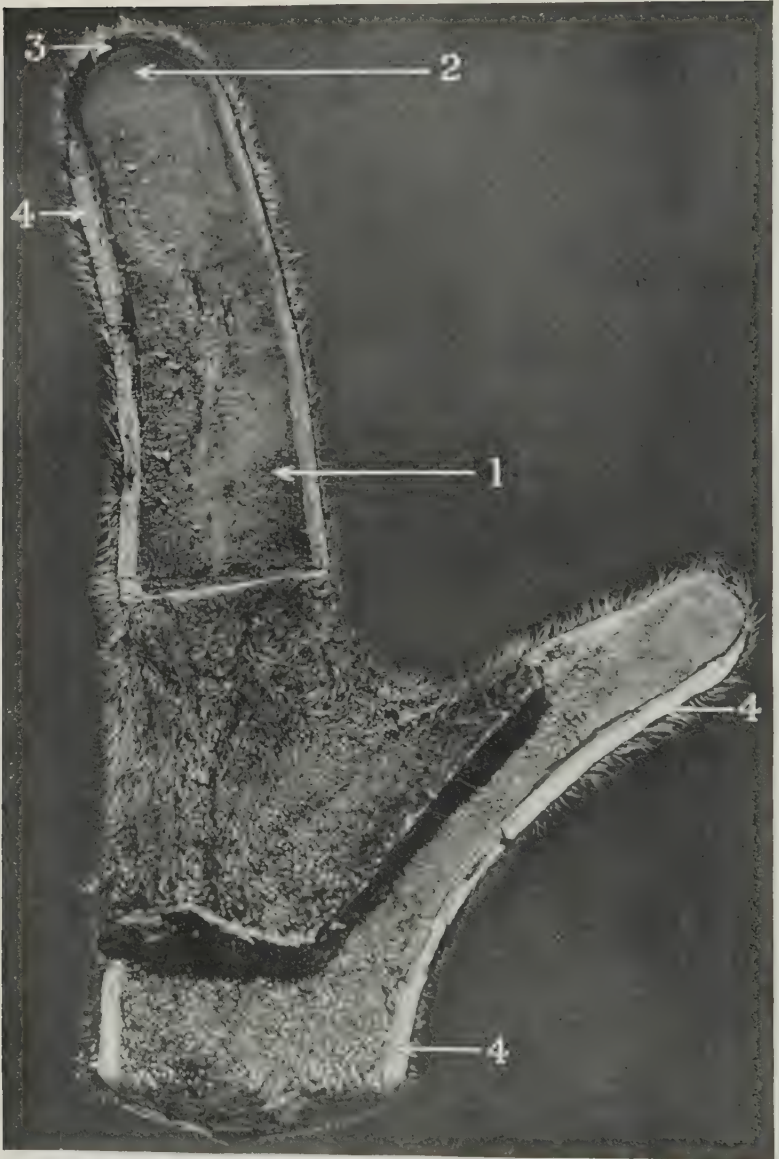


Fig. 26. Longitudinal section of a four months' old antler. The undifferentiated connective tissue tip has been replaced by new directly formed bone; 1. Body or core of new directly formed compact bone; 2. Complete hardening and ossification of undifferentiated connective tissue tip; 3. Velvet of tip is dark, shriveled and dead. This is a point at which shedding of velvet begins; 4. Living velvet below the tip.

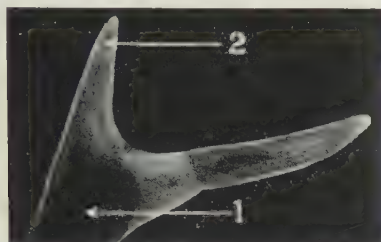


Fig. 27. Completely ossified tip of mature antler; 1. Spongy area of interior; 2. Completely ossified tip.

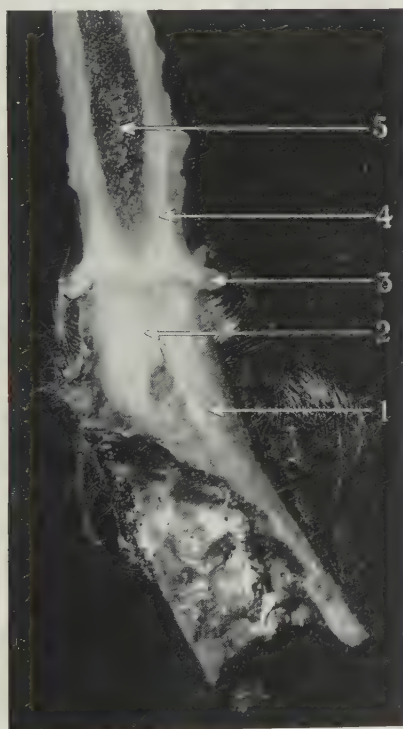


Fig. 28. Longitudinal section of mature antler and pedicle. (Six months' old); 1. Frontal bone; 2. Pedicle; 3. Burr or corona; 4. Compact bone wall and base of mature antler; no velvet is present; 5. Spongy porous character of interior of antler.



Fig. 29. External view of the tip of an elk antler 75 days old. Note the hair of the velvet.



Fig. 30. Internal view of the antler of figure 29 on longitudinal section; 1. The ossifying core of undifferentiated connective tissue, richly supplied with blood and containing areas in process of direct ossification together with small areas of new formed bone; 2. Rapidly proliferating undifferentiated connective tissue, embryonic in character, forming the growing tip of the antler; 3. Proliferating undifferentiated connective tissue continuing down the side of the antler tip; 4. The layer of velvet enveloping the antler.

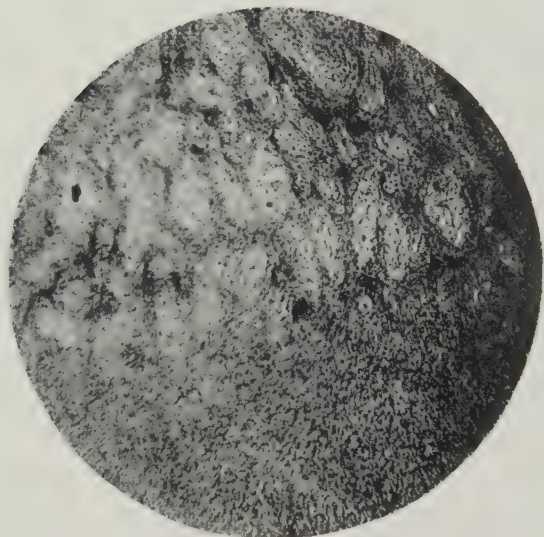


Fig. 31. Cross section 3.5 cm. from tip, ossification beginning peripherally. Obj. 16 mm. apochro. Ocular $8\times$ comp.

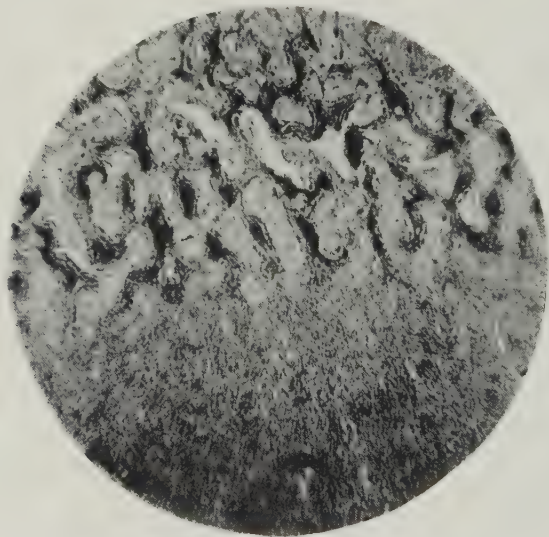


Fig. 32. Cross section 4.5 cm. from tip showing pronounced peripheral ossification. Obj. 16 mm. apochro. Ocular $8\times$ comp.

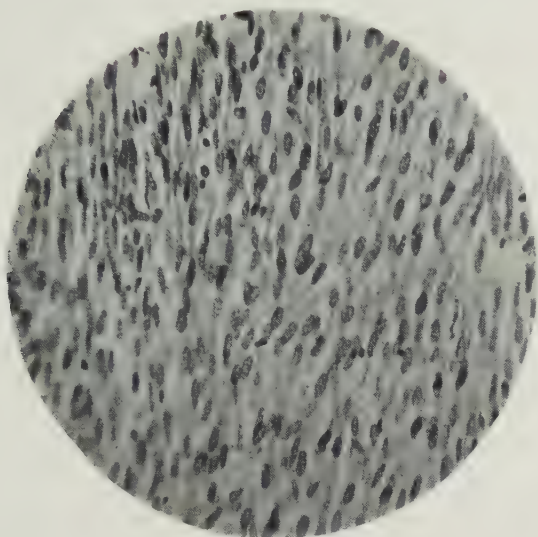


Fig. 33. Section through undifferentiated connective tissue showing typical spindle-shaped fibroblastic cells. Obj. 4 mm. Ocular 8 \times comp.

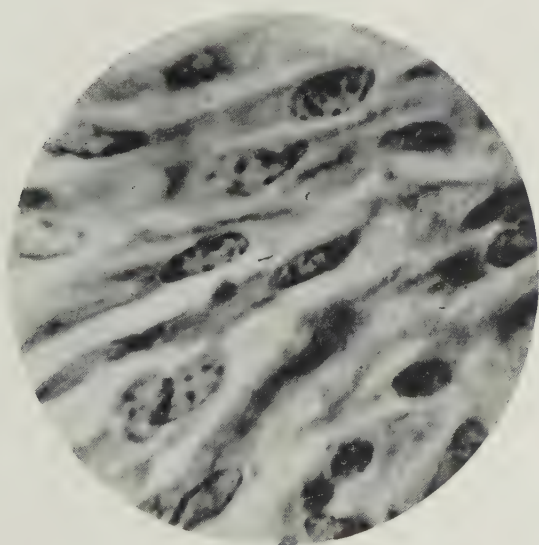


Fig. 34. Typical fibroblastic cells of the cap under oil immersion. Obj. 2 mm. (oil imm.). Ocular 8 \times comp.



Fig. 35. Longitudinal section 1.5 cm. from tip showing evolving fibroblasts, endothelial cells and beginning blood channels. Obj. 32 mm. Ocular 8 \times comp.



Fig. 36. Longitudinal section 1.5 cm. from tip showing evolving fibroblasts, endothelial cells and beginning blood channels. Obj. 16 mm. Ocular 8 \times comp.

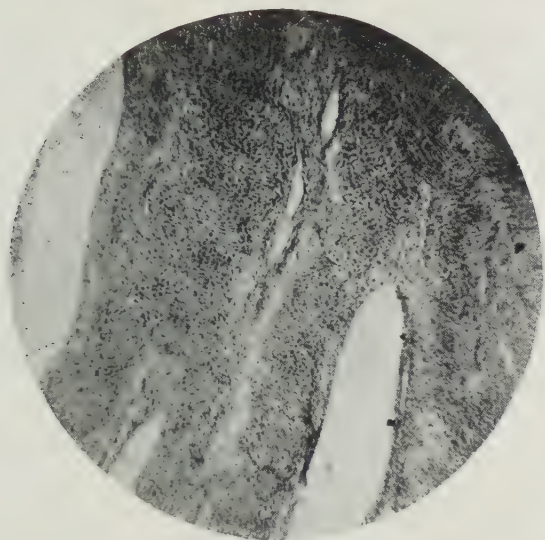


Fig. 37. Longitudinal section 2.0 cm. from tip showing evolving fibroblasts and open blood channels. Obj. 32 mm. Ocular 8 \times comp.

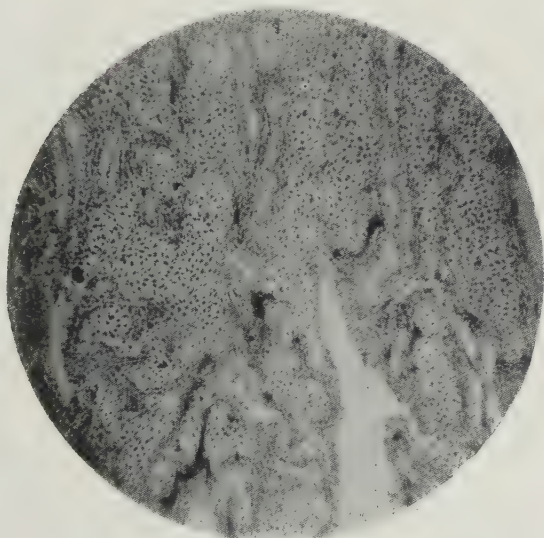


Fig. 38. Longitudinal section 2.5 cm. from tip showing maturing fibroblasts, open blood channels and slight centres of ossification. Obj. 32 mm. Ocular 8 \times comp.

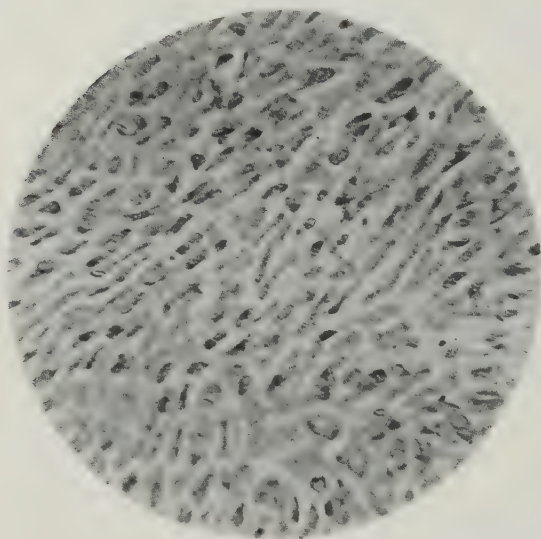


Fig. 39. Typical fibroblastic cells 1.5 cm. from tip. Obj. 4 mm. Ocular 8 \times comp.

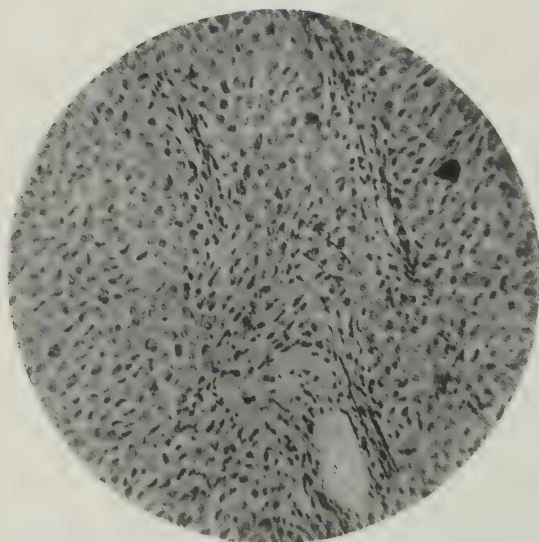


Fig. 40. Cells 2.5 cm. from tip showing maturing fibroblasts and endothelial cells. Obj. 16 mm. Ocular 8 \times comp.

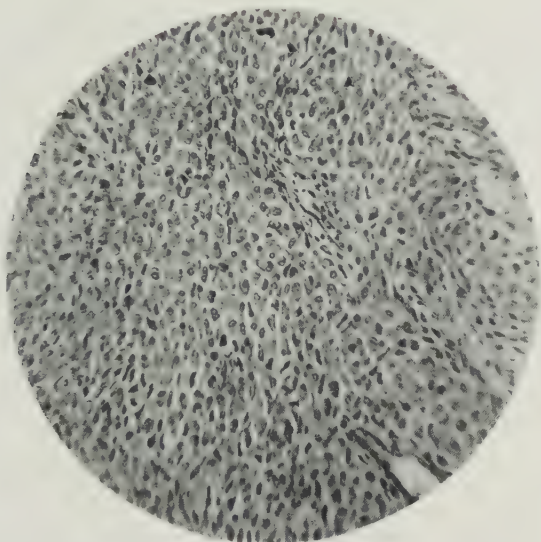


Fig. 41. Cells 2.5. cm. from tip showing matured fibroblasts and endothelial cells. Obj. 16 mm. Ocular 8 \times comp.

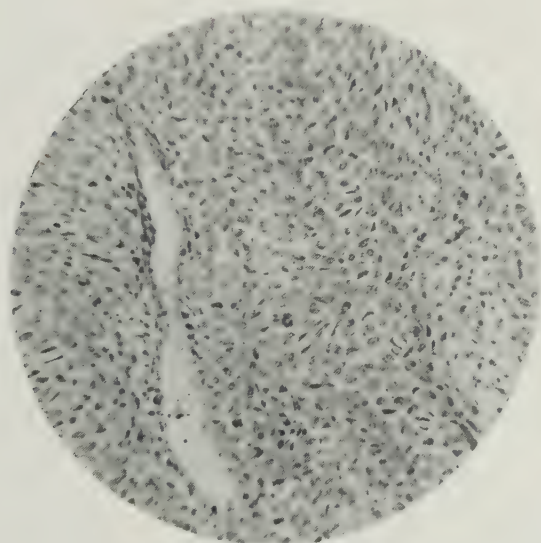


Fig. 42. Cells 3.0 cm. from tip showing matured fibroblasts, a few of which have atrophied. Obj. 16 mm. Ocular 8 \times comp.

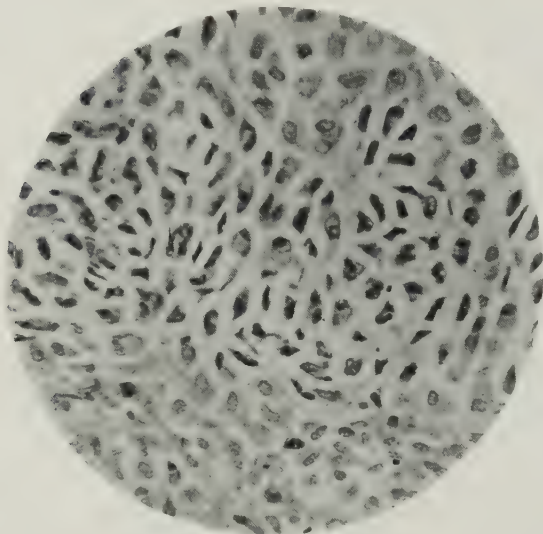


Fig. 43. Cells 3.5 cm. from tip showing marked atrophy of some fibroblasts and separation of the cells. Obj. 4 mm. Ocular 8 \times comp.

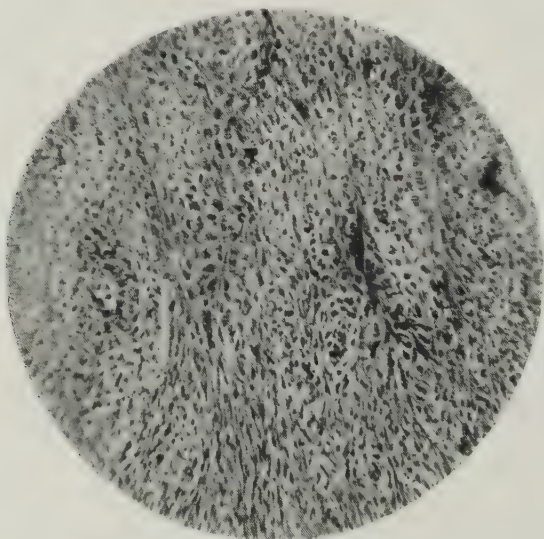


Fig. 44. Cross section 2.5 cm. from tip. Osteoblasts proliferating from periphery to centres of ossification. Obj. 16 mm. Ocular 8 \times comp.

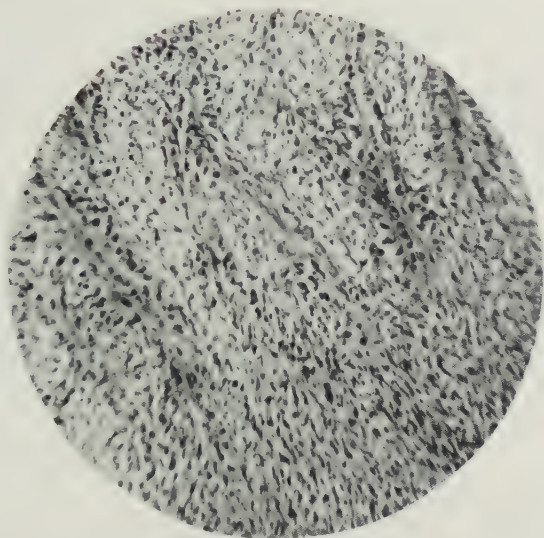


Fig. 45. Cross section 3 cm. from tip. Osteoblasts proliferating from periphery to centres of ossification. Obj. 16 mm. Ocular 8 \times comp.

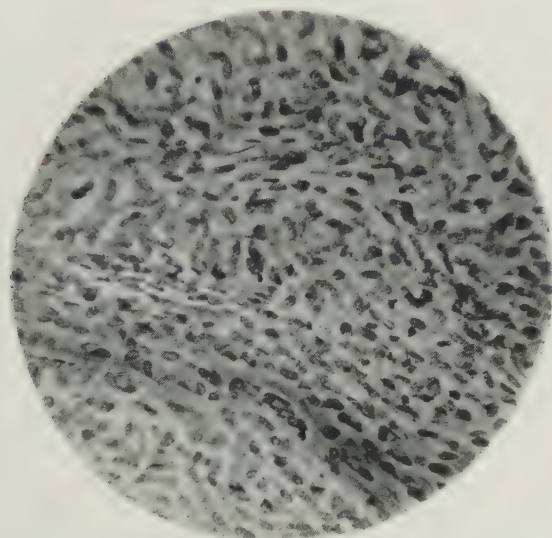


Fig. 46. Section 3.0 cm. from tip. Peripherally derived osteoblasts around centre of ossification. Obj. 4 mm. Ocular 8 \times comp.

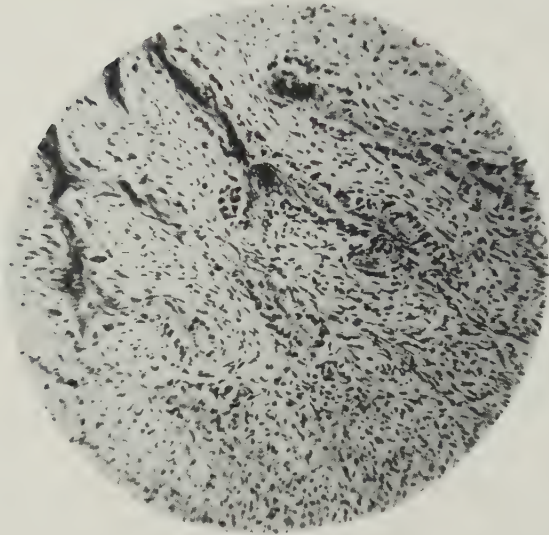


Fig. 47. Cross section 3.5 cm. from tip. Osteoblasts proliferating from periphery to centres of ossification. Obj. 16 mm. Ocular $8\times$ comp.

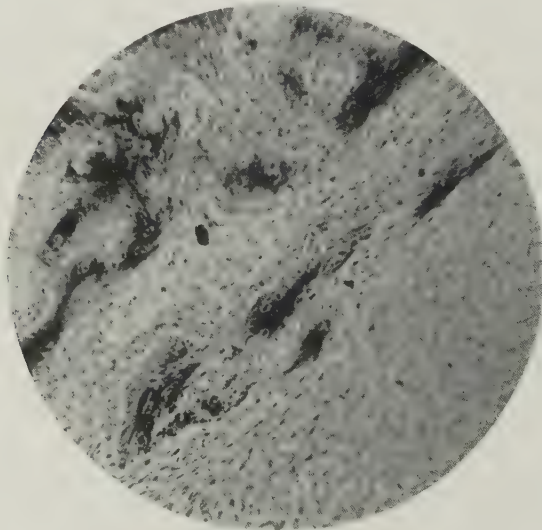


Fig. 48. Longitudinal section 4 cm. from tip showing proliferation of peripherally derived osteoblasts and lacunae in centres of ossification. Obj. 16 mm. Ocular $8\times$ comp.



Fig. 49. Longitudinal section 5 cm. from tip showing proliferation of peripherally derived osteoblasts. Obj. 16 mm. Ocular 8 \times comp.

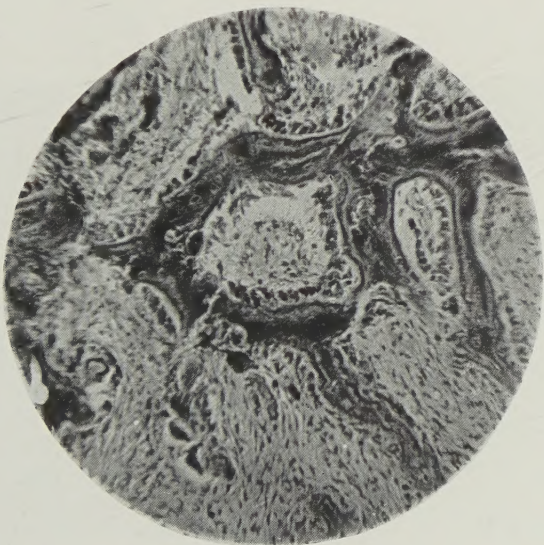


Fig. 50. Cross section 5.0 cm. from tip showing proliferation of osteoblasts and mature osteoblasts between blood channels and trabeculae. Obj. 16 mm. Ocular 8 \times comp.

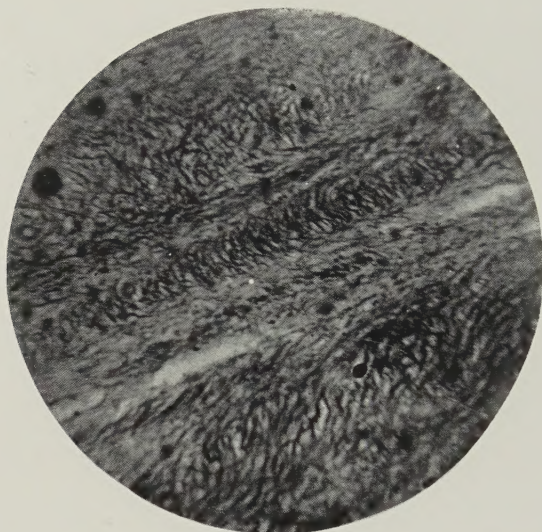


Fig. 51. Showing fibrillar structure of cap continuous with fibers of velvet. Obj. 16 mm. Ocular 8 \times comp. Stain: Modified Del Rio Hortega's Silver Carbonate Method.

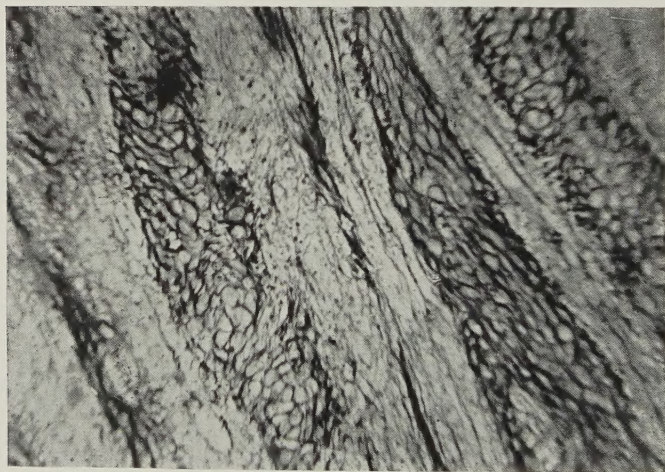


Fig. 52. Showing fibrillar ground-work 2.0 cm. from tip and longitudinal fibrillae of blood channels. Obj. 4 mm. Ocular 8 \times comp. Stain: Modified Del Rio Hortega's Silver Carbonate Method.

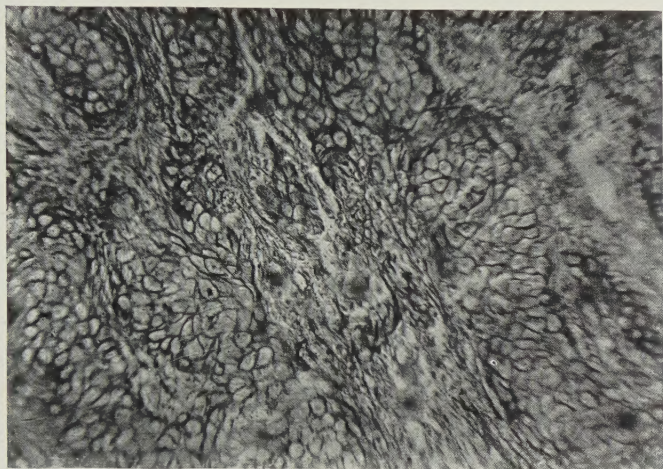


Fig. 53. Fibrillar network 3 cm. from tip. Obj. 4 mm. Ocular 8 \times comp. Stain: Modified Del Rio Hortega's Silver Carbonate Method.

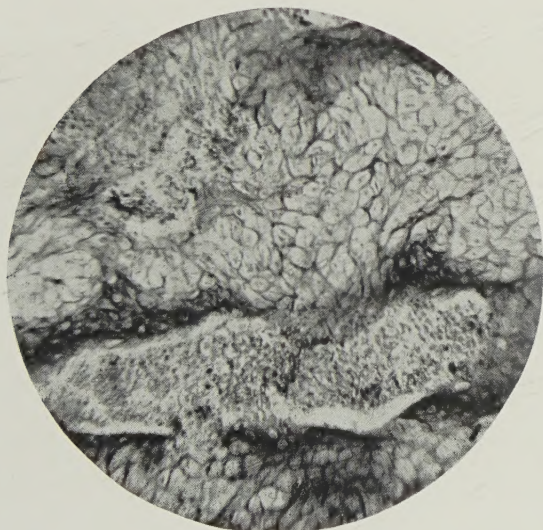


Fig. 54. Fibrillar network 4 cm. from tip. Note blood in blood channels. Obj. 4 mm. Ocular 8 \times comp. Stain: Modified Del Rio Hortega's Silver Carbonate Method.

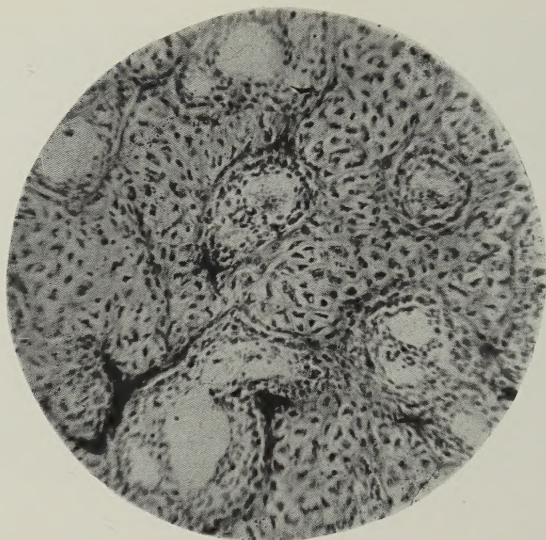


Fig. 55. Cross section 3.5 cm. from tip showing atrophy of fibroblasts derived from the cap and slight centres of ossification.

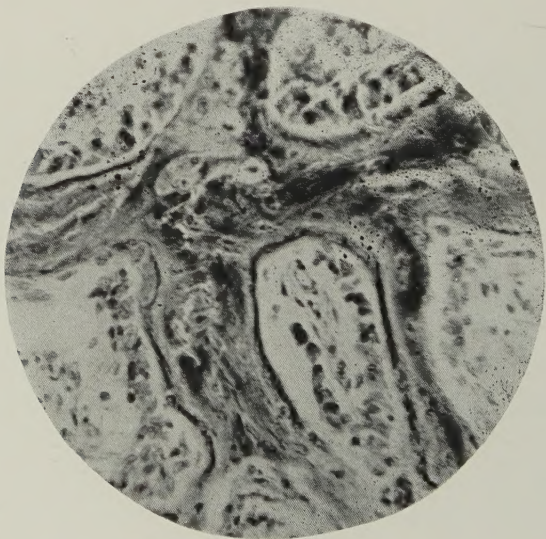


Fig. 56. Cross section 5.0 cm. from tip showing definitive osteoblasts evolved from peripheral undifferentiated connective tissue. Obj. 4 mm. Ocular 8 \times comp.